REPRODUCTIVE DECISIONS BY BLACK BRANT: MECHANISMS TO SYNCHRONIZE HATCH AND SPATIAL VARIATION IN GROWTH RATES OF GOSLINGS

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A

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By

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ABSTRACT

I investigated two aspects of reproductive decisions in Black Brant: synchronous hatch within clutches and areas in which to rear their broods. It has been hypothesized that *Anatidae* facilitate a synchronous hatch through vocalizations among embryos within the same clutch. I performed manipulative experiments in which variation was controlled for both genetic and incubation pattern sources in incubation period length. Our results suggest that vocalizations are not responsible for a synchronous hatch, and I suggest that inherent properties of the eggs themselves are responsible for a synchronous hatch. Additionally, I compared gosling growth rates from areas of low nest densities with those from a main colony to test the hypothesis that broods using dispersed areas were escaping density dependent effects. I found that goslings from dispersed nesting areas did not escape density dependent effects and may actually constitute a sink for the population from additional effects of increased nest mortality in dispersed nesting areas.

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ACKNOWLEDGEMENTS

Both chapters of this Masters of Science thesis are written in journal format in preparation for submission. Chapter 1 is intended for submission in *Functional Ecology* and Chapter 2 for submission to *The Journal of Wildlife Management.* This thesis is single authored, although co-authors for each manuscript are referenced on the first page of each chapter. The "we" in each chapter refers to all authors referenced.

Although this thesis presents original ideas from myself and others, I feel they would have not have been as fully developed without the advice of Dr. Jim Sedinger. Even before this thesis was realized, Jim was, and continues to be, a source of encouragement. I know I am stubborn in my progress as a waterfowl biologist, but I am confident that my time spent with Jim will greatly improve my abilities. I would also like to thank my committee members, Dr. Roger Ruess and Dr. Perry Barboza. I thoroughly enjoyed discussions with both, and they contributed greatly to my knowledge of the systems of both chapters in this thesis.

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INTRODUCTION

Successful reproductive strategies are key components of fitness in individuals. We investigated two aspects of reproduction, and I present the results of these two studies for my thesis. Both of the two chapters that follow are formatted for publication in peer reviewed journals. Although there are multiple authors on both chapters, I take full responsibility for any errors.

The first aspect of reproduction I studied is the timing of initiation of incubation, which is a key decision for individuals. In geese, females begin incubation after the second egg is laid, yet some mechanism exists to facilitate a synchronous hatch. It has been hypothesized that waterfowl induce a synchronous hatch through vocalizations by first laid embryos as hatching begins. In my first chapter, we explored the mechanisms that may allow a synchronous hatch. We experimentally manipulated clutches in two ways: 1) We assembled clutches in which all eggs were from the same position in the laying sequence, laid on the same day, and came from different females, and 2) We assembled clutches in which the full compliment of positions in the laying sequence was maintained, but all originated from different females at the same stage of laying. In addition, we monitored a set of control nests in which no eggs were manipulated. By manipulating clutches in these two ways, we were able to control for both genetic and environmental or maternal effects upon incubation duration.

Additionally, we measured O_2 consumption (ml O_2/hour) of eggs in the latter half of incubation using closed system respirometry. We tested the working hypothesis that metabolic rates are a proximate means to facilitate a synchronous hatch.

The second aspect of successful reproduction we studied is decisions brant make to raise young. Location of brood rearing areas, and furthermore, quality of brood rearing areas have many implications for several life history traits and population-level implications. Adult body size, fledging survival, and fecundity have been shown to be influenced by first-year growth in goslings. The second chapter of this thesis investigates growth rates of black brant goslings from two areas of dispersed nesting and we compare these rates to those of a main colony nesting area. We monitored nests in the study areas until hatch, at which time we marked goslings with individually coded fish-fingerling tags. Concurrent with banding efforts, we recaptured a sample of these marked goslings and measured mass, tarsus length, and culmen length.

Approximately 20% of the entire black brant population nests in these dispersed areas, and it is of management concern to quantify reproductive parameters in this segment of the population.

CHAPTER 1. Regulation of development time and hatch synchronization in Black Brant (*Branta bernicla nigricans*).[1]

Summary

1. Eggs of precocial bird clutches hatch more synchronously than they are laid. The widely accepted hypothesis to explain hatching synchrony has been that vocalizations from earlier laid embryos accelerate development of later laid embryos. We investigated the relationship between position in the laying sequence and time to hatching in Black Brant (*Branta bernicla nigricans*; hereafter brant). We also examined factors associated with variation in duration of incubation.

2. We assembled experimental clutches comprised of eggs laid on the same day from the same position in the laying sequence (hereafter PILS) to eliminate the effects of earlier laid eggs on those laid later. This experiment allowed us to examine development time in clutches consisting of eggs all laid on the same day and in the same position in the laying sequence, thereby removing effects of interactions between eggs laid earlier in the sequence and those laid later. In a separate experiment, we manipulated clutches so that the full complement of laying sequences was maintained in each clutch, but each egg in a clutch originated from a different female. This experiment allowed us to separate the influences of genetic and maternal effects from the influence of nest environment and

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incubation behavior. We also monitored development time in a set of clutches that were unmanipulated.

3. We measured metabolic rates of eggs from each position in the laying sequence from both experimental and control nests at mid-incubation and the day before hatch. By measuring metabolic rates, we were able to examine changes in metabolic rates of embryos as hatch approaches, which may be another mechanism to synchronize hatch.

4. We detected no difference between control nests and manipulated clutches in time to begin hatching. There was a steady decline in time required to reach hatching from first to last-laid eggs independent of the type of clutch in which they were incubated. Eggs laid fifth in the sequence required >3 days less to develop than those laid first, independent of their incubation environment. These data suggest that sounds produced by brood mates and/or incubation patterns by the female are not the principal mechanisms for hatching synchrony within a clutch. Both genetic and host mothers influenced overall development time, indicating that genetic-maternal effects and incubation behavior and nest environment also influenced development time.

5. Metabolic rate of embryos was negatively correlated with number of days before hatch, but there was not a positive relationship between position in the laying sequence and metabolic rate. Our findings show that embryonic metabolic rate may affect development more than vocalizations between brood members in synchronizing hatch.

Key-words: Alaska, Black Brant, *Branta bernicla nigricans*, egg, hatching synchrony, incubation, metabolism

Introduction

Hatching of most Anatidae usually occurs within a short time period (3-24 hours; Afton and Paulus 1992; Johnson 1974; McKinney 1969; Munro and Bedard 1977; Weller 1964), because hatching synchrony is essential to reproductive success (Afton and Paulus 1992; Flint et al. 1994; Rohwer 1992). It is a commonly held hypothesis that Anatidae begin incubation after laying the final egg in a clutch (Cramp and Simmons 1977; Johnsgard 1975; Kear 1970; Kendeigh 1952; Weller 1964). This hypothesis probably originated from observations of synchronous hatch, which was thought to require a mechanism beginning with a synchronous initiation of incubation (Cargill and Cooke 1981). In several Anatidae species (Lesser Snow Geese, *Chen caerulescens caerulescens*: Afton and Paulus 1992; Cooke, Findlay & Rockwell 1984; Krechmar and Syroechkovsky 1978; Syroechkovsky 1975; Mallards, *Anas platyrhynchos*: Caldwell and Cornwell 1975; Eldridge and Krapu 1988; Prince, Siegel & Cornwell 1969; Canada Geese, *Branta canadensis maxima*: Cooper and Hicken 1972; and Black Brant: Flint et al. 1994), eggs tend to hatch in the order in which they are laid, suggesting that effective incubation begins before the clutch is complete. In several species of Anatidae, effective incubation begins before all eggs within a clutch are laid (Afton 1978; Caldwell and Cornwell 1975; Cargill and Cooke 1981; Cooper 1978; Eisenhower 1977; Krechmar and Syroechkovsky 1978; Persson and Andersson 1999), as early as the laying of the second egg (Flint et al. 1994). Many studies have shown that female nest attendance, which produces temperatures sufficient to induce embryonic development (Funk and Biellier 1944; Haftorn 1988; Lundy 1969), increases during laying (Afton 1980; Caldwell and

Cornwell 1975; Cargill and Cooke 1981; Cooper 1978 and 1979; Shurakov 1978). Therefore, upon completion of laying, eggs within a clutch vary in stage of development (Afton and Paulus 1992). Because all eggs within a clutch hatch within a 24-hour period, embryos from eggs laid after the second must develop faster than first-laid eggs. Several studies have hypothesized that vocalizations by first-laid embryos stimulate embryos in later laid eggs to accelerate their development, allowing them to hatch synchronously (Freeman and Vince 1974; Persson and Andersson 1999; Vince 1969).

In most Anatidae, egg size increases from first to second eggs, then declines with position in the laying sequence (hereafter PILS; Ankney and Bissett 1976; Cooper 1978; Flint and Sedinger 1992), and among species, variation in incubation length is positively correlated with egg size (Arnold 1993). Flint et al. (1994) proposed a model, in which effective incubation begins with the laying of the second egg, laying intervals after the second egg progressively decrease, whereby the clutch hatches more synchronously than expected. Flint et al. (1994) further suggested that because first-laid eggs in brant clutches receive up to 48 hours of incubation before the last egg is laid, yet all eggs within the clutch hatch in a 24 hour period, some mechanism reduces developmental asynchrony during incubation.

If time required for development is associated with the rate of metabolic processes in embryos, we might also expect variation in metabolic rates among eggs in a clutch (Hoyt et al. 1979; Vleck and Vleck 1980). MacCluskie, Flint & Sedinger (1997) found that mallard embryos varied substantially in metabolic rate, and that embryos produced by different females varied substantially (>2 days) in development time when reared in

standardized conditions. However, Slattery and Alisauskas (1995) showed that goslings from later-laid eggs within a clutch hatched in a less fully developed state. These results suggest that properties of the eggs or embryos themselves could explain variation in development rate and time.

Because goslings hatch with less than 4 days of energy reserves (Ankney and Bisset 1976), even a 2-day spread in hatch dates could reduce survival probability of first-hatched goslings. Additionally, hatching synchrony may reduce variation in growth among brood mates (Arnold, Rohwer & Armstrong 1987; Friedl 1993) and reduce the exposure period of the nest to predators (Flint et. al 1994). Understanding mechanisms of hatching synchrony is thus essential to fully understand reproductive adaptations.

We examined two hypotheses to explain hatching synchrony. The vocalization hypothesis states that embryos from earlier laid eggs accelerate hatch of later laid embryos through vocalizations as hatch approaches (Driver 1965; Persson and Andersson 1999). We predicted that if goslings synchronize hatch through inter-egg communication, there would be no mean difference in development time among eggs in clutches representing a single PILS collected from a number of clutches, after controlling for egg size. Our rationale is that removing stimulating effects of early eggs on later ones would lengthen the development time of later laid eggs to equal that of early laid eggs.

The second hypothesis is that embryos from eggs later in the laying sequence develop more rapidly than the embryos from earlier laid eggs. Under this hypothesis, we predicted that embryos from later laid eggs in the laying sequence would have higher metabolic rates and would hatch after a shorter incubation period than embryos from

earlier in the laying sequence. We also examined effects of genetic and host females to evaluate maternal effects and the roles of nest environment and incubation behavior on development time.

Materials and Methods

STUDY SITE

We conducted this experiment during the summers of 1999 and 2000 at the Big Slough Black Brant satellite colony, on the Yukon-Kuskokwim Delta in western Alaska (61°11'N, 165°36'W). This satellite colony is approximately 8 km south of the Tutakoke River Black Brant colony (Sedinger et al. 1993).

CLUTCH MANIPULATIONS

New one-egg nests were located daily and we assumed that the egg was laid on the day it was found. Because we searched the same areas methodically every day, this was a reasonable assumption. We continued daily nest searches until the laying period ended. We manipulated clutches in two ways; (1) to test the vocalization hypothesis; and (2) to separate the effect of genetic mothers from nest environment and incubation behavior. We maintained a third group of unmanipulated nests to serve as controls.

To test the hypothesis that vocalizations from more advanced embryos synchronize hatch, we removed eggs from nests as they were laid in 1999. In 2000, we delayed manipulations until a two-day interval of no egg laying occurred, which indicated cessation of laying within a clutch. This delay in 2000 enabled us to manipulate larger, more complete clutches than in 1999 because we experienced substantial partial predation rates during laying by Glaucous Gulls (*Larus hyperboreus*).

In this experiment, we placed eggs from the same PILS laid on the same day into a randomly selected nest from which eggs had been removed. We thus formed experimental clutches of 4 to 6 eggs, all of which were from the same PILS (Fig. 1). We predicted that if vocalizations were the principal mechanism for synchronizing hatch, when eggs were incubated with other eggs from the same PILS, all eggs would require the same amount of incubation to hatch. In contrast, if inherent properties of eggs were the most important determinate of development time, clutches produced from eggs laid later in the sequence would hatch after less incubation. This experiment also allowed us to partially separate genetic or maternal effects from incubation behavior and nest environment effects because host females were randomly selected and each genetic mother's eggs were incubated by four to six different females.

We also produced a set of experimental clutches containing eggs from the full compliment of PILS, which we refer to as the female effect experiment. In this experiment, we also removed eggs from clutches at cessation of laying for the clutch, but experimental clutches were constructed to contain eggs from each PILS. Eggs were randomly assigned to a host female such that hosts had laid none of the eggs they incubated (Fig. 2). If vocalizations were important for synchronizing hatch, we predicted that eggs laid late in the sequence would require less incubation than in the previous experiment because they were potentially exposed to vocalizations from embryos earlier in the laying sequence. This experiment also separated genetic/maternal effects from incubation behavior and nest environment. Additionally, we monitored a set of control clutches in which no eggs were transferred among females.

Egg length and width were measured to the nearest 0.1 mm using dial calipers and egg volume was calculated following Flint and Sedinger (1992). Eggs were moved between nests in small coolers filled with down and containing a hot water bottle.

METABOLIC MEASUREMENTS

We used closed-circuit respirometry to estimate metabolic rates of embryos (MacCluskie et al. 1997; Scholander 1950,) on both the 17th day of incubation and the day before hatch for the eggs from clutches we manipulated. Day before hatch was determined by candling eggs (Weller 1956). A different sample of eggs was used for measurements in each of these two periods. Our closed-circuit respirometer consisted of two 300 ml glass jars connected by plastic tubing containing a small amount of colored water (Scholander 1950). The jar in which an egg was placed also had 1cm of Ascarite to absorb CO_2 produced by the embryo. One ml of ambient temperature and pressure, pure O_2 was injected into the jar containing the egg. We then measured the time (seconds) for the jar containing the egg to equilibrate to ambient pressure. Three metabolic rate measurements were taken for each egg during a trial. We adjusted O_2 volume to standard temperature and pressure before analysis. Eggs were maintained for a minimum of 20 minutes before the trials and also during the trials in an Igloo brand thermoelectric heater/cooler (Lake Forest, Illinois; model #99) that maintained a constant temperature of 38° C (±1° C). Trials were conducted in a small tent within the study area. Eggs were transported in a small cooler with a warm water bottle and brant down as insulation and were returned to their host nests after the trial.

STATISTICAL ANALYSIS OF MANIPULATED NESTS

We used the mixed model procedure (PROC MIXED) in SAS (1989) and the Satterthwaite method (Kuehl 2000) for calculating denominator degrees of freedom. A maximum likelihood approach was used for parameter estimation. We performed separate analyses for each of the two clutch manipulations and the control nests because the structure of the data did not allow us to analyze them together. Number of days between date laid and date of star pipping was used as the dependent variable. Star pipping is the first star shaped crack in the shell made by the embryos at the beginning of the hatching process.

In the control experiment, PILS and egg volume were used as covariates (Flint and Sedinger 1992). Both the identity of the host and the genetic mother were random class variables. Year was used as a class variable in the Vocalization Experiment as this experiment was tested in two years. We tested all possible combinations of models for each experiment and compared models with AICc (Akaike's Information Criterion, adjusted for small sample size; Burnham and Anderson 1998). We also examined model weights of each model for each experiment. We used model weights to examine the importance of variables within the candidate model set (i.e. sums of model weights for models in which the tested variable was present; Burnham and Anderson 1998).

We examined sources of variation in the selected models by first using the covariance parameter estimates from the results of the mixed model to estimate variation within the random variables. Next, we analyzed the same data set using a linear model (PROC GLM, SAS 1989) and estimated the variance for fixed effects and error. We

allowed the sums of the covariance parameter estimates from the mixed model to equal the error sums of squares from the linear model, while maintaining the proportions of the covariance parameter estimates. We present variance components from mixed model analysis of variance to allow an assessment of the contributions of variables to the overall variance in the dependent variable. We do not use the variance components to test hypotheses in the traditional sense, however, because such hypothesis tests are not consistent with the information theoretic approaches we used to assess models (Burnham and Anderson 1998).

STATISTICAL ANALYSIS OF METABOLIC RATES

The mixed model procedure (PROC MIXED) in SAS (1989) using the Satterthwaite method (Kuehl 2000) and a maximum likelihood approach for parameter estimation were used in analysis of metabolic rates (ml O_2/hour) for the three manipulation types (control, vocalization, and female effect). The volume of O_2 consumed per hour was the dependent variable, with manipulation type as a class variable, and number of days before hatch in which metabolic rates were performed, PILS and egg volume as covariates. Identity of the individual egg was used as a random variable to control for variation among the three samples collected during each metabolic trial. We tested all two-way interactions among class variables and covariates. Additionally, we tested the correlation between the residuals of this analysis against the number of days of incubation required to hatch using a regression approach to examine the relationship between embryo metabolism and development time. We tested all possible combinations of models and compared models using an information theoretic

approach (Aikaike's Information Criterion adjusted for small sample sizes, AICc; Burnham and Anderson 1998).

Results

LENGTH OF INCUBATION PERIOD

Samples of 250 and 280 nests were manipulated in 1999 and 2000, respectively. A year effect was detected for the vocalization manipulation (Table 1) in which a 0.74-day (Fig. 3) increase in incubation length was estimated for clutches manipulated in 1999. Because we manipulated nests in the vocalization experiment differently in the two years, we don't know whether this difference in length of the incubation period was due to an actual difference between years or a result of differences in our manipulation methods. Length of incubation varied nearly identically with PILS for the two sets of experimental clutches and controls (Fig. 3). The exception was the fifth-laid egg, for which eggs in the female effect experiment required 0.81 days less incubation than in the other two experiments. Across all experiments, development time declined linearly from 26.2 days for first eggs to 22-23 days for fifth eggs. The random class variables (host and genetic) we used in the two manipulative experiments (female effect and vocalization) explained a significant amount of variation in incubation period length (sums of model weights containing these terms in both analyses = 1.00; Tables 1 and 2), indicating that genetic and maternal effects and incubation behavior or nest attributes affected development time (Table 1). Egg volume was not a source of significant additional variation after controlling for PILS and genetic mother in the control and female effect manipulations, because models we tested with egg size alone competed poorly when

compared to models in which we controlled for PILS (Table 1). However, egg volume was a significant source of variation in the vocalization experiment which may have been an effect of a larger sample of nests for the vocalization experiment. To facilitate comparison among manipulation treatments, we present results from a more reduced model that did not contain egg volume (Fig. 3; ΔAICc = 2.0).

METABOLIC RATES

Metabolic measurements were based on a sample of 163 eggs in 2000. The number of days before hatch that metabolic rates were sampled and manipulation treatment were significant sources of variation in rate of O_2 uptake (Table 3). We present results from a more parsimonious model than the selected model which contains effects of egg volume (Fig. 4). O_2 consumption rate was negatively correlated with the number of days before hatch that the metabolic rates were sampled (Fig. 4). Due to the relatively small sample sizes within clutch manipulation types, we were unable to control for genetic or host variation in analysis of metabolic rates. When we examined the residual variance from the aforementioned analyses and time required for incubation within each egg, there was a weak relationship, suggesting that metabolic rate did not control for stage of incubation (Fig. 5).

Variation of egg size with PILS was consistent with other studies (Ankney and Bissett 1976; Cooper 1978; Flint and Sedinger 1992) that described an increase in egg size to the second egg, followed by a decline in egg size in the remainder of the clutch.

Discussion

Embryos from eggs laid late in the laying sequence did not measurably accelerate development when exposed to eggs laid early in the sequence. While we cannot rule out the possibility that vocalizations fine-tuned hatching synchrony, over a range of a few hours, our results demonstrate that vocalizations by embryos cannot explain hatching synchrony in waterfowl clutches when embryos varied by up to three days in incubation time. The three-day reduction in incubation required by fifth eggs compared to first eggs in all treatments indicates that properties of the embryos themselves were principally responsible for hatching synchrony. If communication among embryos were the principal mechanism underlying hatching synchrony, we would have expected a lengthening in the required incubation time for eggs later in the laying sequence when incubated only with eggs from the same position in the laying sequence.

Eggs produced by different females required significantly different development times even when incubated by random hosts. These results are consistent with MacCluskie et al. (1997), who also found that eggs produced by different females had inherently different development times, indicating that either genetic or maternal effects substantially influenced development time of embryos. Host female effects (i.e., incubation constancy, nest quality, or nest site location) also explained significant variation in development time. We can think of no advantage to increased development time, but two hypotheses can be applied to explain variation in development time of embryos among genetic mothers. Perhaps maturity at hatch, which influences prefledgling survival (Slattery and Alisauskas 1995), is a trade-off against length of time

an embryo remains in the egg. This trade-off is potentially associated with laying date. There is a fitness advantage to being the first to hatch within a season (Cooch et al. 1991, Sedinger et al. 1995), and Eichholz and Sedinger (1998) showed that eggs of later initiating females required less time to hatch. An alternative hypothesis is that the physiological state of the embryo is somehow matched to the nutritional status of the mother, which influences her incubation constancy (Eichholz and Sedinger 1998), such that the unique development time of an embryo approximates that expected from the incubation behavior of the mother.

Egg conductance and ratio of surface area to volume of eggs place an upper limit on embryo metabolism and may influence development time (Rahn, Paganelli & Ar 1974). Visschedijk (1968) presented an equation that predicted the rate at which gases diffuse through the eggshell. He described two factors that describe diffusion of gases between the shell interior and nest environment: (1) conductance of the eggshell; and (2) differences in gas tension between the inside and outside of the shell. Additionally, many studies have shown an asymptotic upper limit of O_2 consumption for eggs of precocial birds (Vleck and Vleck 1996).

An increase in egg size from the first to second egg, then followed by a decline in egg size progressively in the laying sequences, is consistent with previous studies (Ankney and Bissett 1976; Cooper 1978; Sedinger and Flint 1991). There is considerable additional intraspecific variation in egg size in Anatidae. Coefficients of variation are about 9-11%, most of which are due to variation among females (Rohwer 1986). Little is known about how much of this variation is genetically determined, except for Lesser

Snow Geese (Findlay and Cooke 1987) and Black Brant (Flint, Grand & Sedinger 1996; M. Herzog unpubl. data). Potential sources of non-heritable variation in egg size may include covariation with body size and age (Flint and Sedinger 1992; Flint et al. 1996).

Egg size influences development time in two ways. First, embryos from smaller eggs are themselves smaller and should require less development time (Rahn et al. 1974). Additionally, smaller eggs have a greater ratio of surface area to volume, which enables higher mass-specific rates of O_2 transfer to the embryo (Rahn et. al 1974) and higher rates of metabolism in embryos from later in the laying sequence (Vleck and Vleck 1987). Therefore, we suggest that the decrease in the size of eggs in Anatidae as laying progresses proximately contributes to hatching synchrony. Slattery and Alisauskas (1995) showed that neonate Lesser Snow Geese and Ross' Geese (*Chen rossi*) from eggs later in the laying sequence were less developed (i.e., had higher water muscle content) than those from earlier in the laying sequence, which also would contribute to increased hatching synchrony. Producing smaller eggs likely has a cost because goslings from such eggs are smaller at fledging (Herzog 2002), which in turn influences numerous life-history traits, including adult body size (Sedinger et al. 1995; Larsson and Forslund 1991) and fecundity (Cooch et al. 1991).

In conclusion, the decline in egg size as laying progresses could contribute to hatching synchrony. Later embryos from later-laid eggs in a clutch tend to have higher metabolic rates which we hypothesize also contributes to relatively more rapid development in later embryos, and thus, hatching synchrony. We found that among-embryo vocalizations played a relatively minor role in hatching synchrony. At present,

we are uncertain of the mechanism underlying variation in embryo metabolic rates. Endocrine differences among embryos might explain the observed variation (Rahn et al. 1974). Potentially, endocrine variation exists among PILS. We point out, however, that there must be some cost to faster development, because selection pressure to reduce incubation time and associated predation should favor the most rapid development possible, other things being equal (Flint et al. 1994; Persson and Andersson 1999). Variation among females in behavioral and genetic or maternal regulation of development suggests a tradeoff between development rate and other life-history traits or a constraint on female's ability to increase development rate. The rate of development as indicated by O_2 consumption is relatively constant across embryos from different PILS. Therefore, the tradeoff is between time of development (synchrony) and tissue maturation.

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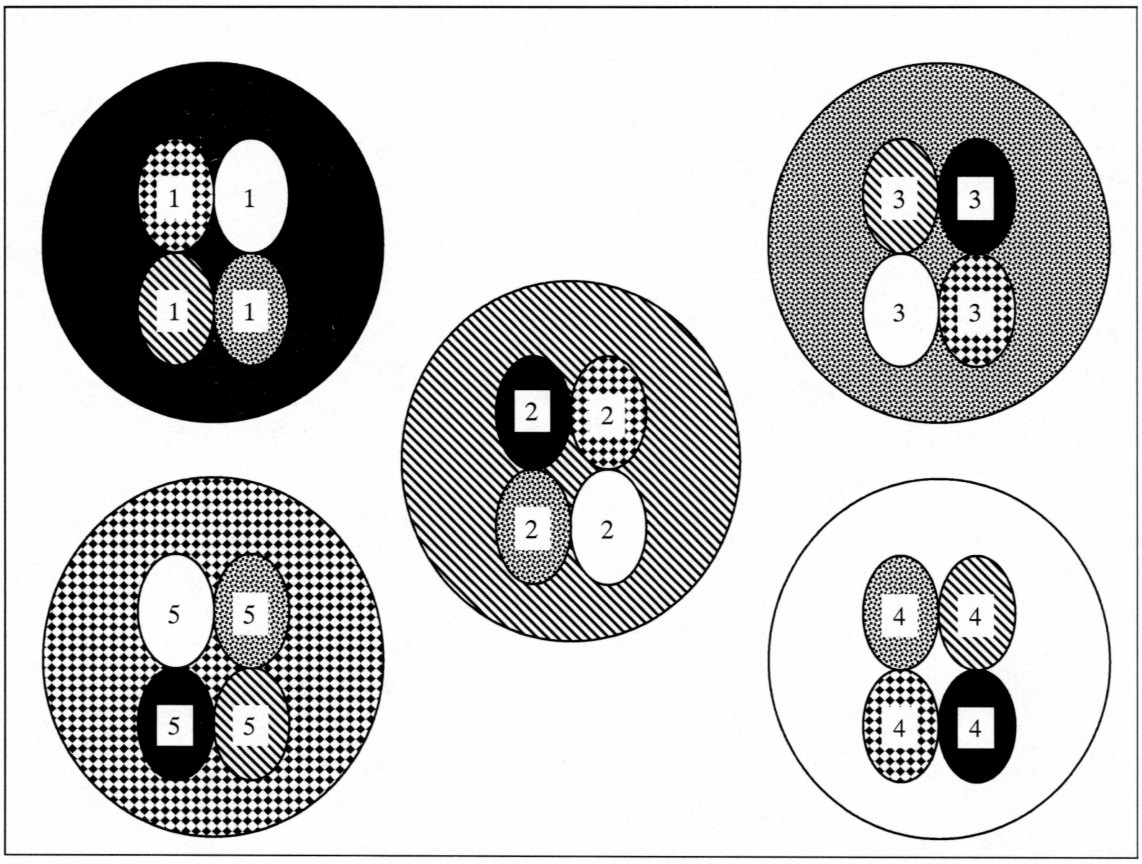

Fig. 1-1. Diagram of egg manipulations for the test of the vocalization hypothesis for which we created clutches in which all eggs were from the same position in the laying sequence, were laid on the same day, and all originated from different females. Different shadings refer to different females (nests) and numbers refer to position in the laying sequence.

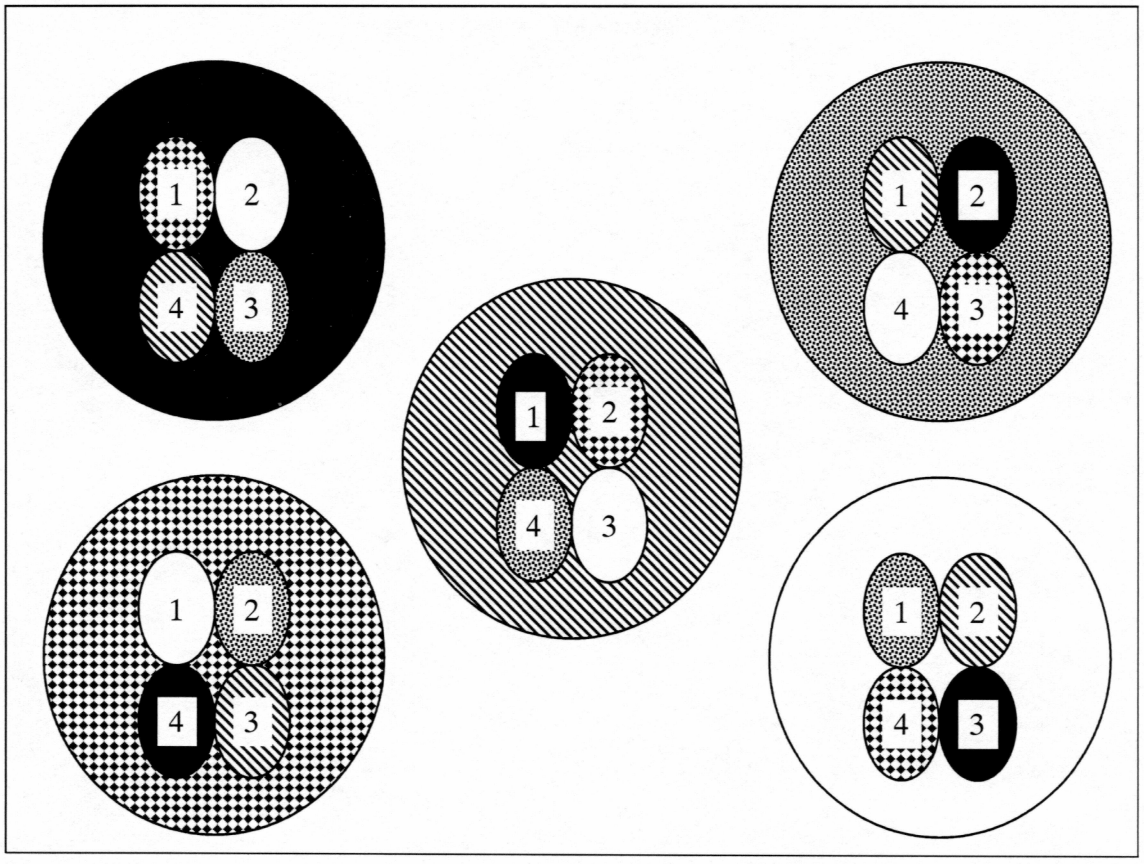

Fig. 1-2. Diagram of egg manipulations for the female effect hypothesis in which we created clutches that maintained the full compliment of positions in the laying sequence, but eggs originated from different females. Different shadings refer to different females (nests) and numbers refer to the position in the laying sequence.

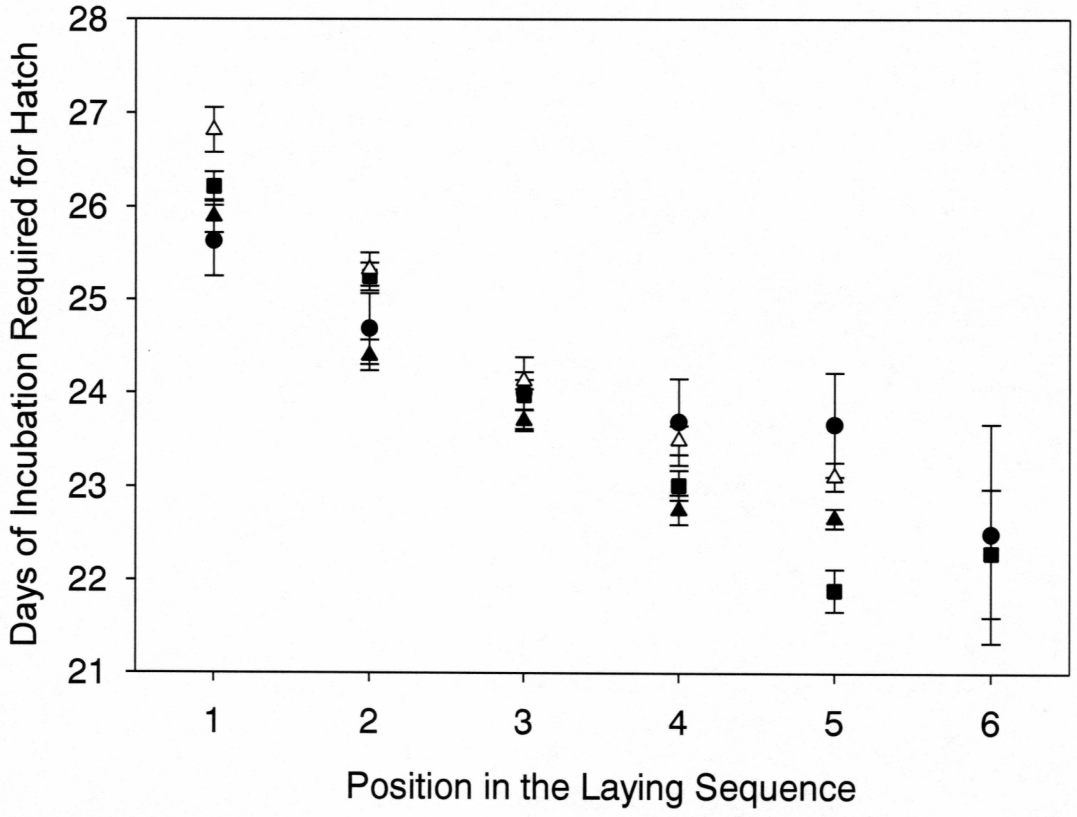

Fig. 1-3. Results of length of incubation period analysis using position in the laying sequence as a class variable. LSMeans and SE are presented for control and female effect nests. Means and SE are presented for vocalization nests. Circles represent control nests, squares represent female effect nests, dark triangles represent vocalization nests from 2000, and open triangles represent vocalization nests from 1999.

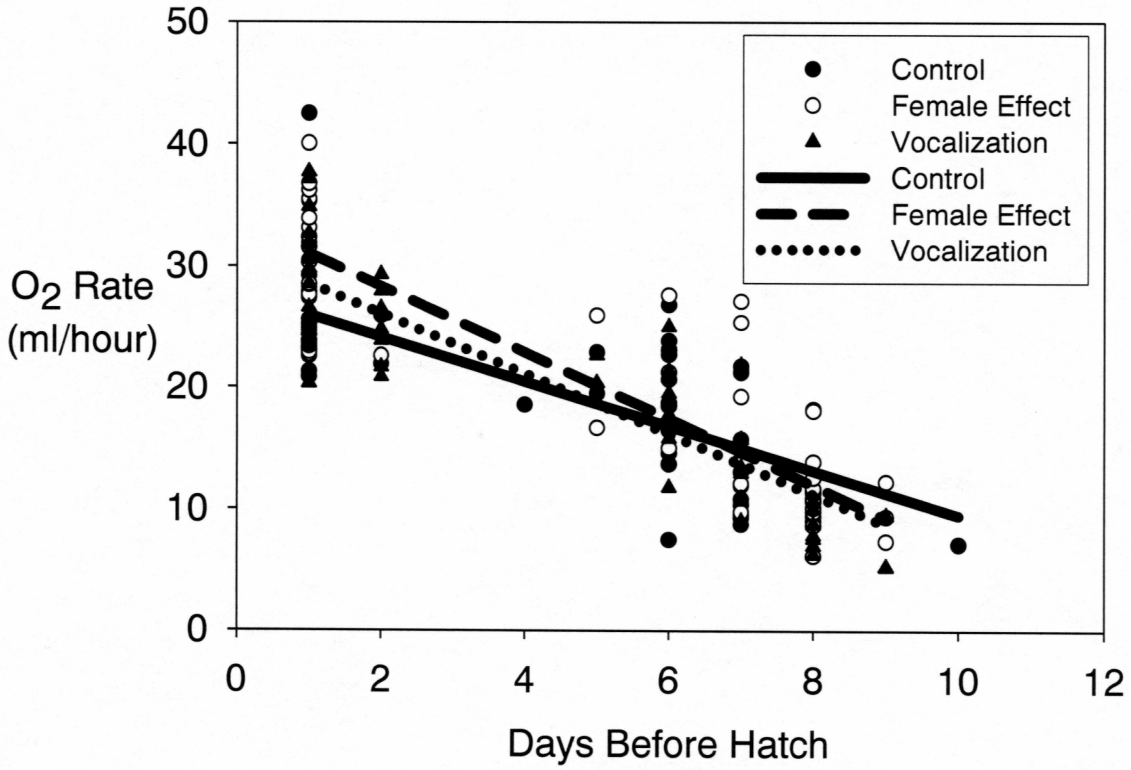

Fig. 1-4. Results of metabolic rate analysis. Dots represent metabolic rates averaged across the three samples for each trial. Lines are regressions for each manipulation type.

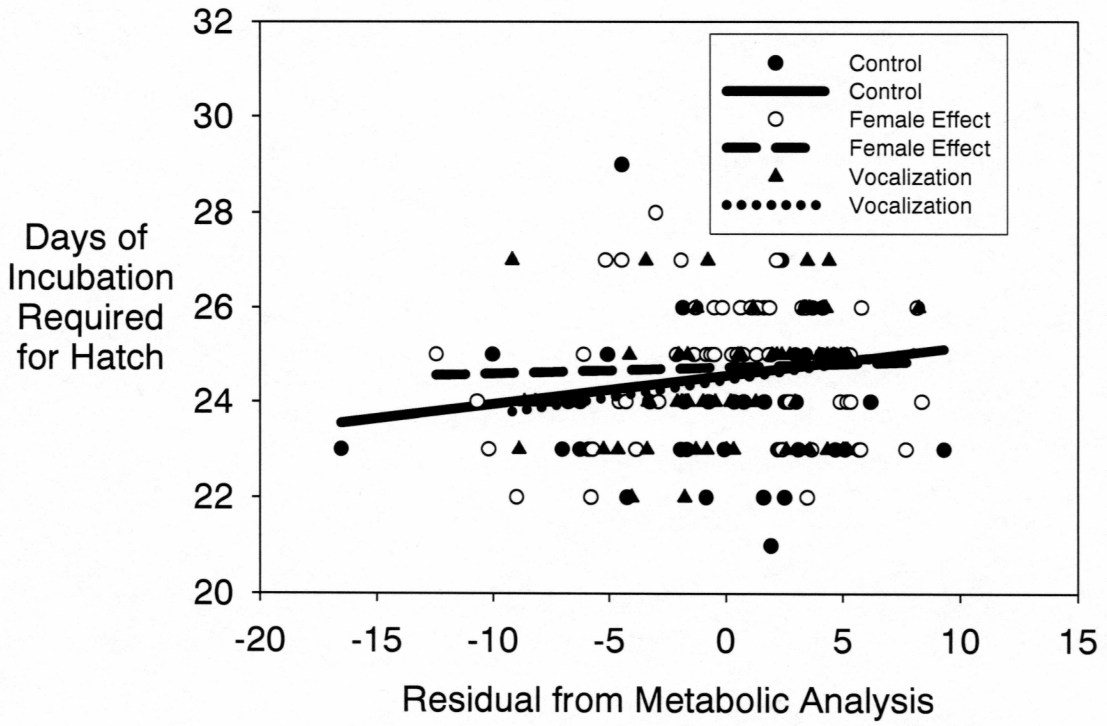

Fig. 1-5. Residuals of metabolic rate analysis compared to incubation time required for each egg to hatch.

Table 1-1. Mixed model results for incubation period.

Experiment	Model[a]	AICc	ΔAICc	Model Weight
Control[b]	PILS+G	298.2	0.0	0.4933
	PILS+ES+(PILS*ES)+G	298.8	0.6	0.3654
	PILS+ES+G	300.7	2.5	0.1413
	PILS	337.4	39.2	0.0000
Female Effect	PILS+H+G	283.2	0.0	0.7250
	PILS+ES+H+G	285.6	2.4	0.2184
	PILS	426.4	143.2	0.0000
Vocalization	PILS+ES+Year+H(PILS)+G	966.1	0.0	0.3316
	PILS+ES+Year+(PILS*ES)+(ES*Year) +H(PILS)+G	966.3	0.2	0.3077
	PILS+ES+Year+(ES*Year) +H(PILS)+G	967.3	1.2	0.1866
	PILS+YEAR+H(PILS)+G	968.1	2.0	0.1251
	PILS+ES+Year	1201.1	235.0	0.0000

[a] PILS = Position in the laying sequence. ES = Eggsize (volume). Host (H) is a random variable in the mixed model controlling for within host female effects. Genetic (G) is a random variable in the mixed model controlling for within genetic female effects.

[b] Genetic and Host effects cannot be separated in this experiment because they are one in the same.

Table 1-2. Mixed model variance partitioning for incubation length. Values are percentages of total variance within each experiment.

	Experiment		
Effect	Control	Female Effect	Vocalization
PILS	20.4	64.9	55.2
Year			4.7
Host*		3.7	29.9
Genetic	57.5	24.3	4.3
Residual	22.1	7.1	6.7

*In the vocalization experiment, PILS is nested within Host effects.

Table 1-3. Mixed model results for metabolic rate analysis.

Model[a]	AICc	ΔAICc	Model Weight
Treat+DBH+ES+(Treat*DBH)+(Treat*ES)+(DBH*ES)+Egg	2791.7	0.0	0.5798
Treat+DBH+(Treat*DBH)+Egg	2793.7	2.0	0.2133
DBH+ES+(DBH*ES)+Egg	2797.0	5.3	0.0410
DBH+ES+(DBH*ES)	2976.4	184.7	0.0000

[a] Treat = Manipulation treatment. DBH = # of days metabolic rate was taken before hatch. ES = Egg size (volume). Egg is used as a random variable to control for variation among three samples for each metabolic rate trial.

CHAPTER 2. DO BLACK BRANT GOSLINGS FROM SATELLITE COLONIES ON THE YUKON-KUSKOKWIM DELTA, ALASKA EXPERIENCE REDUCED DENSITY DEPENDENCE?[1]

***Abstract*:** Reduced gosling growth is the principal mechanism by which density influences population dynamics in geese, so we compared growth rates of Black Brant (*Branta bernicla nigricans*) goslings from two satellite colonies and a large colony on the Yukon-Kuskokwim Delta, Alaska during the summers of 1999 and 2000. Approximately 20% of the Black Brant population on the Yukon-Kuskokwim Delta, Alaska nests outside of four major colonies. Dispersal to these outlying breeding locations has been hypothesized as a mechanism to reduce density dependence associated with the major colonies. Gosling growth rates varied among brood rearing areas away from the Tutakoke River colony, and for goslings from brood rearing areas associated with the Tutakoke River colony. Mean size of goslings, adjusted for age, from brood rearing areas associated with satellite colonies ranked sixth, eighth, and ninth out of nine brood rearing areas in 1999, and sixth and ninth out of nine brood rearing areas in 2000. Mean masses of goslings from the brood rearing area associated with a satellite colony with the largest mass were 198 and 139 g smaller than those from brood-rearing areas producing the largest goslings in 1999 and 2000 respectively (both associated with the Tutakoke River Colony). Our findings suggest that goslings from these satellite colonies do not

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benefit from reduced density dependent effects, and therefore, do not have an advantage over goslings from a major colony with respect to recruitment, survival, and adult body size. Combined with low nesting success of Black Brant in dispersed sites, our results suggest that dispersed nesters may constitute a sink for the population.

Key words: Black Brant, *Branta bernicla nigricans*, density dependence, growth rates, Yukon-Kuskokwim Delta

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Gosling growth is highly variable (Aubin et al. 1993, Cooch et al. 1991, Sedinger and Flint 1991) and is governed by quality and quantity of forage plants (Cooch et al. 1991 and 1993, Larsson and Forslund 1991, Loonen et al. 1997, Sedinger et al. 1997, 2001). Density is often negatively correlated with forage availability, and therefore is an important determinant of growth rate in geese (Black et al. 1998, Cooch et al. 1991, Sedinger et al. 1998). Dispersal to lower density brood rearing areas provides a potential mechanism to "escape" from local density dependence. Dispersal to non-traditional brood rearing areas (hereafter BRA) has been described in Lesser Snow Geese (*Chen caerulescens caerulescens*; Cooch et al. 1993), and new colonies of Barnacle Geese (*B. leucopsis*) have formed, which potentially allow breeding in areas of high food availability (Black et al. 1998).

Reduced growth of young at higher population densities is a principal mechanism regulating local populations of geese because first-year survival is highly correlated with body size of goslings late in their first summer (Cooch et al. 1991, Francis and Cooke 1992, Schmutz 1993, Sedinger et al. 1995). Growth rate also affects adult body size

(Cooch et al. 1991, Larson and Forslund 1991, Loonen et al. 1997, Sedinger et al. 1995) and future fecundity (Sedinger et al. 1995). Thus, local breeding density is negatively correlated with both recruitment and fecundity, through its influence on gosling growth. The ability of individuals to reduce density-dependent effects by dispersing to areas of lower density can potentially alter regional population dynamics by increasing both their likelihood of recruitment and future fecundity.

Approximately 75% of the breeding Black Brant (*Branta bernicla nigricans*; hereafter brant) population nests on the Yukon-Kuskokwim (Y-K) Delta (Sedinger et al. 1993). Eighty percent of brant nesting on the Y-K Delta nest in four major colonies and the remainder nest in small aggregations (Sedinger et al. 1993), which we define as satellite colonies, away from these colonies. Numbers of nests in the four major colonies increased from 12000 to >19000 between 1982 and 1992 (Anthony et al. 1992, Sedinger et al. 1993).

Local density, through its impact on food abundance (Person et al. 1998) reduced growth of goslings on the two largest colonies on the Y-K Delta (Sedinger et al. 1998, 2001). Furthermore, numbers of Brant nesting in aggregations outside these four large colonies have increased since 1985 (Stehn unpubl. rept.). If goslings produced in satellite colonies grew more rapidly than those in the major colonies, relatively greater recruitment by these goslings would provide a mechanism explaining the growth of satellite breeding aggregations. We measured growth rates of goslings from two satellite colonies in 1999 and 2000 to test the hypothesis that individuals hatched outside the

largest colonies experienced increased growth rate relative to the main colonies as a result of reduced density dependence.

METHODS

We monitored goslings originating from one large colony (Tutakoke River Colony; hereafter TRC) and two satellite colonies (Big Slough and Aknerkochik River), located on the outer coastal fringe in the central part of the Y-K Delta in western Alaska (Figure 1). Lindberg (pers. comm.) visited the Big Slough satellite colony in 1992 and counted 347 nests. This number increased to 749 nests in 1999 (Wege and Nicolai unpubl. data).

After hatch began at TRC, where color banding has been conducted since 1984, all nests in which at least one parent was marked were visited at least every other day until they hatched. At Big Slough and Aknerkochik, all nests were checked daily for hatching goslings. Individually coded fish-fingerling tags were applied to the foot webbing of hatched goslings and goslings in pipping eggs (Alliston 1975, Sedinger and Flint 1991). Because hatching of individual clutches requires approximately 24 hours, we were able to determine gosling ages to within ±1 day. Following hatch, broods move to rearing areas up to 40 km from nest sites (Lindberg et al. 1997) where they have relatively well-defined home ranges (Flint and Sedinger 1992). Attachment of radios to nesting adult females at hatch in 1999 indicated that most broods at Big Slough moved to one general brood rearing area (Horseshoe Lake), whereas at Aknerkochik River, attachment of radios indicated a more widespread movement of broods to BRAs (Wege and Nicolai unpubl. data). During the adult remigial molt, goslings were subsequently

recaptured in corral traps (Sedinger et al. 1997) at 16-36 days of age, (Figure 1), during a range of ages when growth was approximately linear (Herzog and Sedinger, unpubl.), and before they fledged at about 42 days of age (Bellrose 1980). Areas associated with satellite colonies selected for recapture were chosen because of the presence of radio-marked broods (10 of 10 at Big Slough and 5 of 10 at Aknerkochik River; Wege and Nicolai unpubl. data). We weighed goslings using spring scales (±5g) and measured diagonal tarsus, and total culmen using dial calipers (±0.1 mm; Dzubin and Cooch 1992).

We used the mixed model procedure in SAS (SAS Institute 1989) to assess variation in gosling measurements among BRAs. We included year, sex, and BRA as class variables and age as a covariate. To control for within-brood effects, brood identity was included as a random variable in the analysis. We used a maximum likelihood approach to generate parameter estimates, and the Satterthwaite method (Kuehl 2000) was used to calculate denominator degrees of freedom. We used an information theoretic approach to select the most parsimonious model for the data based on Akaikes's Information Criterion adjusted for small sample size (AICc) (Anderson et al. 2000, Burnham and Anderson 1998).

We examined sources of variation in the selected models by first using the covariance parameter estimates from the results of the mixed model to estimate variation within the random variables. Covariance parameter estimates measure the amount of variance for random effects within residual error. Next, we analyzed the same data set using a linear model (PROC GLM, SAS 1989) and estimated the variance for fixed effects and error. We allowed the sums of the covariance parameter estimates from the

mixed model to equal the error sums of squares from the linear model, while maintaining the proportions of the covariance parameter estimates. We present variance components from mixed model analysis of variance to allow an assessment of the contributions of variables to the overall variance in the dependent variable. We do not use the variance components to test hypotheses in the traditional sense, however, because such hypothesis tests are not consistent with the information theoretic approaches we used to assess models.

RESULTS

We recaptured 487 and 212 goslings from 301 and 158 broods in 1999 and 2000, respectively (Table 1.). We captured goslings on two BRAs associated with Aknerkochik River, two areas associated with Big Slough, and seven areas associated with TRC. Twelve goslings from the TRC were recaptured at brood rearing areas principally associated with the Big Slough satellite colony and six goslings from the Big Slough satellite colony were recaptured at BRAs associated with the TRC.

Five models for gosling mass were within two ΔAICc units of each other (Table 2). We present estimates from a model containing year, sex, BRA, age, brood, and year*BRA (ΔAICc=0.5; Table 2 and Figure 2). Gosling mass varied among BRAs, broods, ages, and between years and sexes. We found a significant interaction between year and BRA (Table 2). Model selection for measurement of tarsus also varied among BRAs, years, sexes, and ages. A model containing two two-way interactions (year*BRA and age*BRA) was selected (Table 2). Similarly, model selection for measures of culmen

also varied among BRAs and ages, and between years and sexes, with year*BRA and age*BRA interactions (Table 2).

As in other studies of gosling growth rates in this population (Sedinger et al. 2001a), males were larger than females. After adjusting for age, males weighed 31.6 ± 5.6 g more than females and had tarsi and culmens that were 2.3 ± 0.3 mm and 0.21 ± 0.12 mm longer than those of females, respectively (Figures 2-4). Goslings of the same age weighed 298.9 ± 64.8 g more and had tarsi and culmens that were 6.2 ± 3.8 mm and 2.3 ± 1.6 mm longer in 1999 than in 2000, respectively (Figures 2-4). In contrast to the hypothesis that goslings from satellite colonies grew faster than those from the TRC, BRAs associated with satellite colonies ranked sixth, eighth, and ninth out of nine BRAs in gosling mass in 1999 and sixth and ninth out of nine BRAs in 2000 (Table 4.). Goslings from the satellite area with the largest size were 198 and 139 g smaller than those from the TRC BRAs producing the largest goslings in 1999 and 2000, respectively, while they were 28 and 44 g smaller than goslings from the TRC BRAs producing the smallest goslings in the two years (Figure 2).

DISCUSSION

Our results demonstrate that growth of goslings varies among BRAs both within and among areas primarily associated with TRC and two satellite colonies. Variation in gosling growth among BRAs occurs in other populations of geese (Aubin et al. 1993, Larsson and Forslund 1991, Sedinger et al. 2001) and has been related to both availability and quality of forage (Cooch et al. 1991, Manseau and Gauthier 1993, Sedinger and Flint

1991, Sedinger et al. 1997). Person et. al (1998) found that forage quantity in these same areas we studied at Tutakoke River varied substantially and the areas Person et. al (1998) found to have highest quantity also had the largest goslings in this study.

Gosling size on BRAs associated with satellite colonies was smaller than, or similar to, that for goslings from the large colony we studied. Our findings, thus, indicate goslings produced in satellite colonies do not experience reduced density dependent effects on their growth. Sedinger et al. (2001) showed that brant goslings from the mid-size brant colony on the Colville River Delta (70°N 149°W) on Alaska's arctic coast were larger than goslings from TRC and the Kochechik Bay colony (62°N 166°W), another major colony on the YKD(~300g difference), suggesting that brant goslings at TRC were well below maximal growth rates in the mid-1990's.

Because gosling growth directly affects first-year survival and consequently recruitment into the breeding population (Cooch et al. 1991, Francis and Cooke 1992, Owen and Black 1989, Sedinger et al. 1995), our findings suggest that recruitment rates are unlikely to be higher for goslings from satellite colonies than those from major colonies. Nest success is lower in satellite than major colonies (Raveling 1989), which was also true during our study. Nest success in the satellite colonies averaged 65% between 1998 and 2000 (Wege and Nicolai unpubl. data) compared to 80% in the TRC (J. Sedinger pers. comm..).

Modeling of dynamics in the Pacific Black Brant population indicates that the combination of nest success and recruitment we observed in satellite colonies may not be adequate to maintain population growth (i.e., $\lambda>1$). Therefore, satellite colonies likely

have been maintained by immigration, likely from the major colonies. Lindberg et al. (1998) estimated natal emigration rates of 34 to 100% for brant nesting in several colonies on the Y-K Delta, while more recent estimates have fluctuated between 1 and 20% (Sedinger unpubl.). Based on reproductive and demographic parameters, approximately 900-1000 female goslings have been produced at TRC and survived to breeding age annually. TRC represents about 25% of total nests in major colonies on the Y-K Delta. Thus, we expect 3,600-4,000 such female goslings are produced on all major colonies on the Y-K Delta, providing a substantial available pool of recruits for satellite colonies. Based on the results of this study we conclude that, while dispersal from major colonies to satellite colonies likely occurs, emigrants do not apparently experience reduced density dependence impacts for their goslings. While growth of satellite nesting areas appears to depend on dispersal from the larger colony, it is not clear that such dispersal increases the rate of population increase through reduced density dependence and increased recruitment.

MANAGEMENT IMPLICATIONS

Our data suggest that recent increases in the number of Black Brant nesting in satellite colonies may result only from recruitment within the satellite colonies, but may be augmented by immigration from main colonies. From a metapopulation view, satellite colonies could be unsustainable patches which are rescued from the main colonies via immigration. Satellite colonies may provide a release for main colonies when nesting densities become too high. From a management perspective, it may not be advantageous to manage directly for satellite colony nesting Black Brant, but rather for the pathways

that allow immigration into these areas when nesting density becomes too high in the main colony nesting areas.

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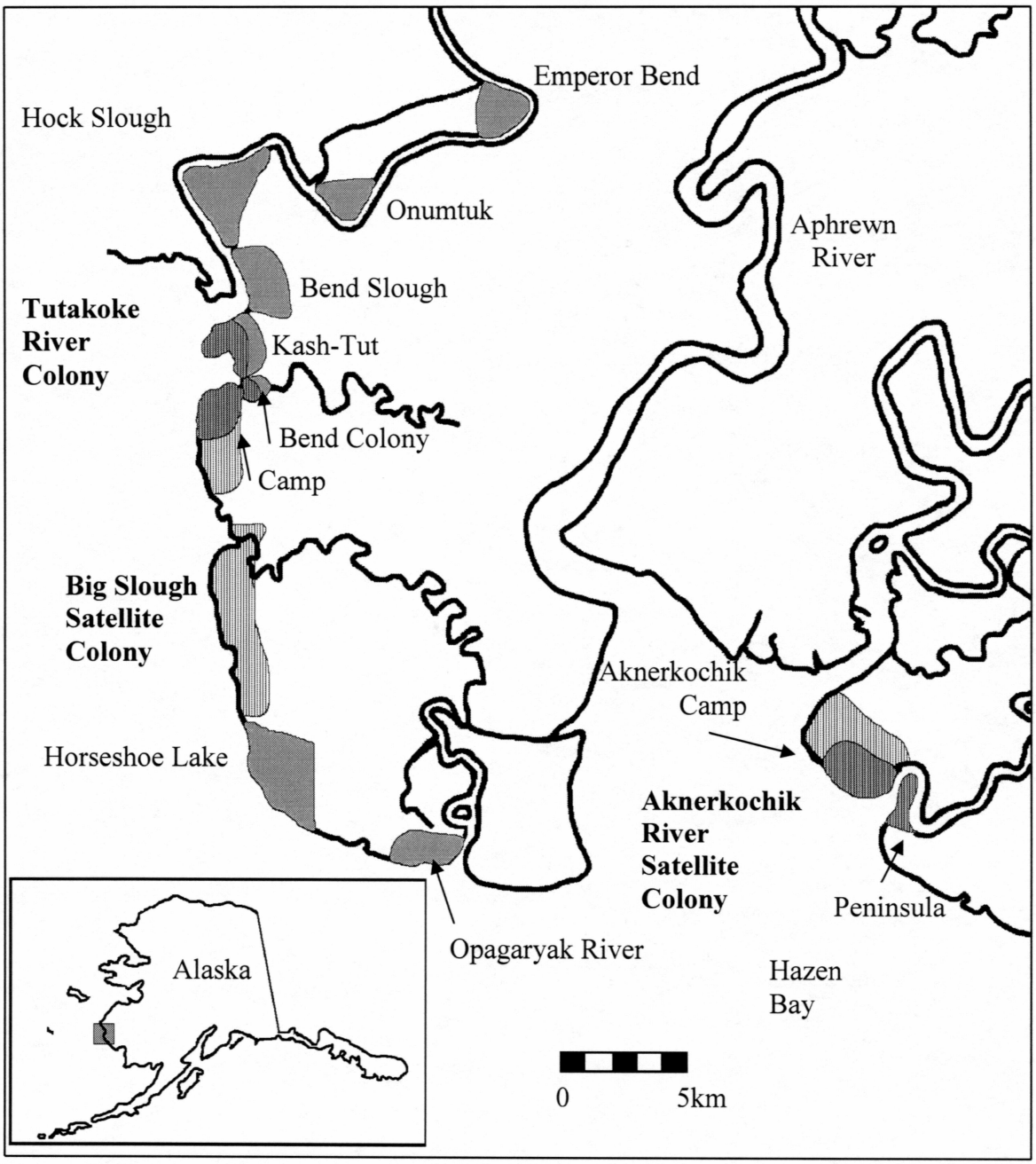

FIGURE 2-1. Location of study and brood rearing areas on the Yukon-Kuskokwim Delta, Alaska. Shaded areas refer to brood rearing areas. Hatched areas and bold type refer to nesting areas where webtags were applied.

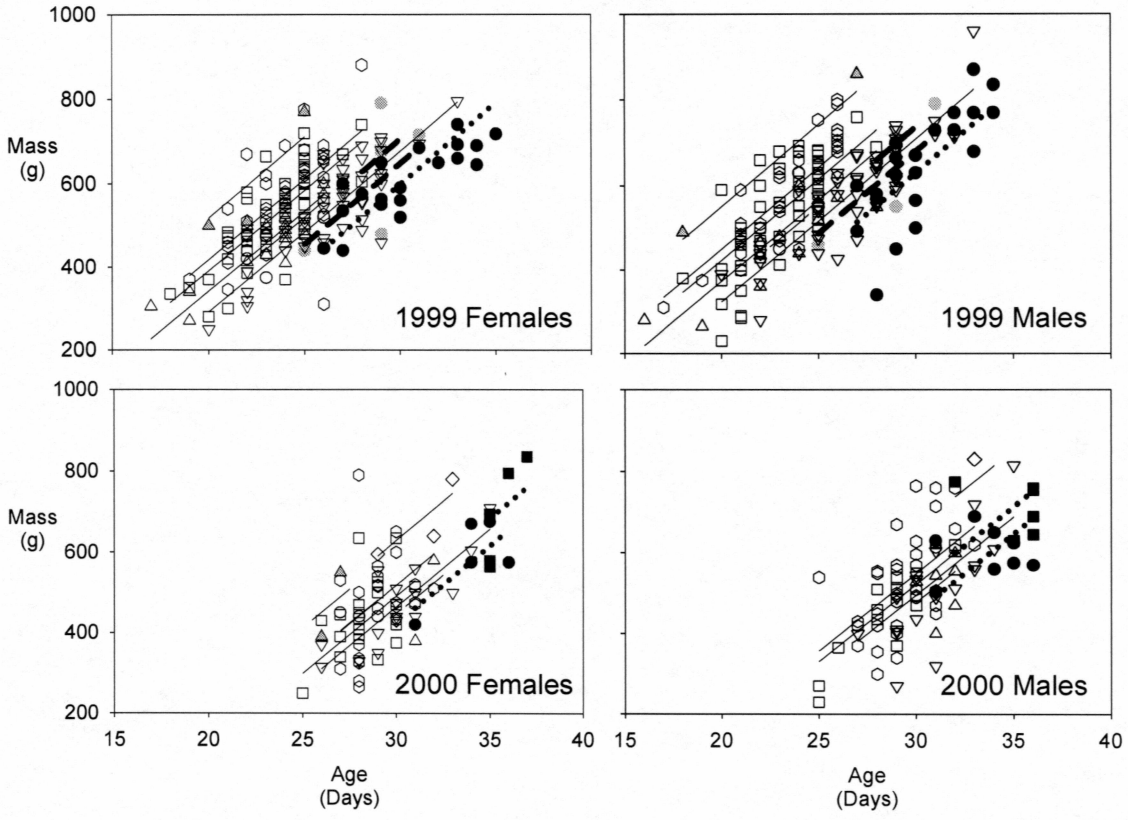

FIGURE 2-2. Gosling mass (g) versus age (days). Grey symbols and dashed lines represent Aknerkochik River. Black symbols and dotted lines represent Big Slough. Open symbols and solid lines represent Tutakoke River Colony. Only individual broods are presented. For presentation, gosling mass was averaged among brood mates within the same year and sex. Aknerkochik River brood rearing areas: ● Camp, ■ Peninsula. Big Slough brood rearing areas: ● Horseshoe Lake, ■ Opagaryak River. Tutakoke River Colony: ○Bend Colony, □Bend Slough, △Camp, ▽Emperor Bend, ◇Hock Slough, ⬡Kash-Tut, and ▲Onumtuk.

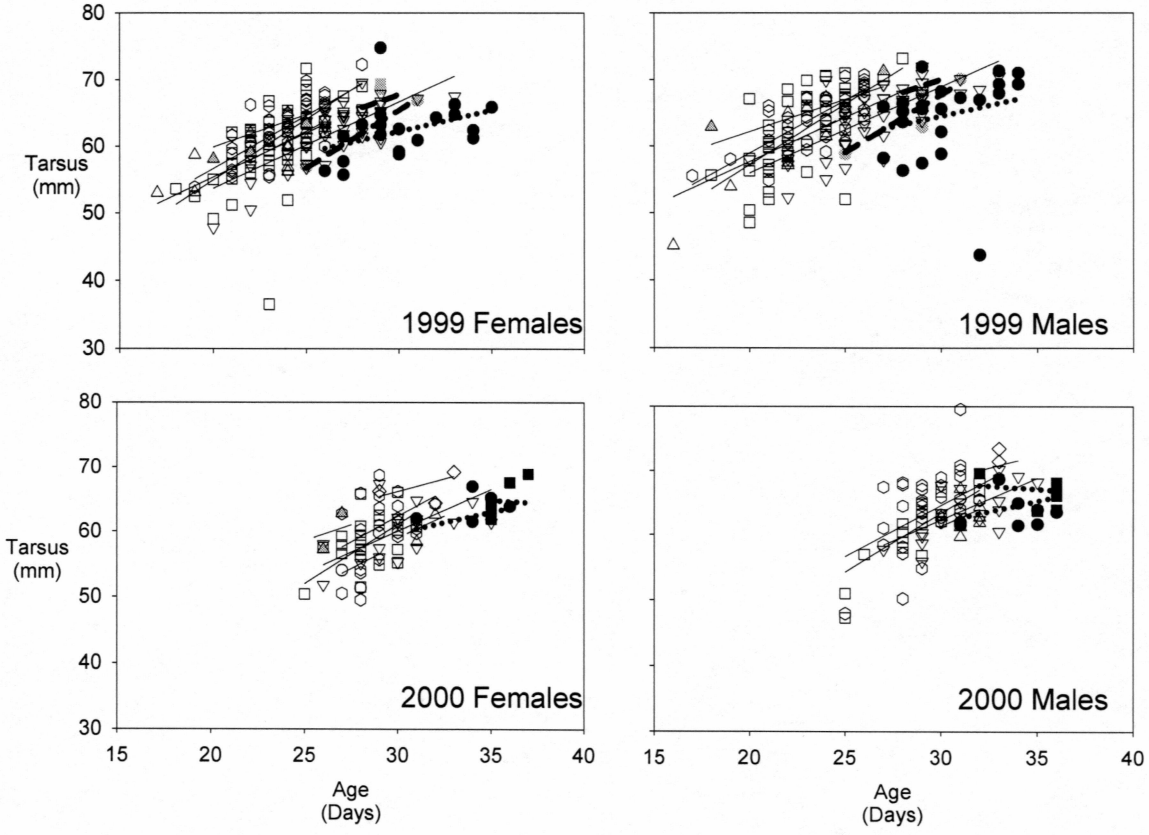

FIGURE 2-3. Gosling tarsus length (mm) versus age (days). Dashed lines represent Aknerkochik River, dotted lines represent Big Slough, and solid lines represent Tutakoke River Colony. Only individual broods are presented. For presentation, gosling tarsus length was averaged among brood mates within the same year and sex. Aknerkochik River brood rearing areas: ● Camp, ■ Peninsula. Big Slough brood rearing areas: ● Horseshoe Lake, ■ Opagaryak River. Tutakoke River Colony: ○ Bend Colony, □ Bend Slough, △ Camp, ▽ Emperor Bend, ◇ Hock Slough, ⬡ Kash-Tut, and ▲ Onumtuk.

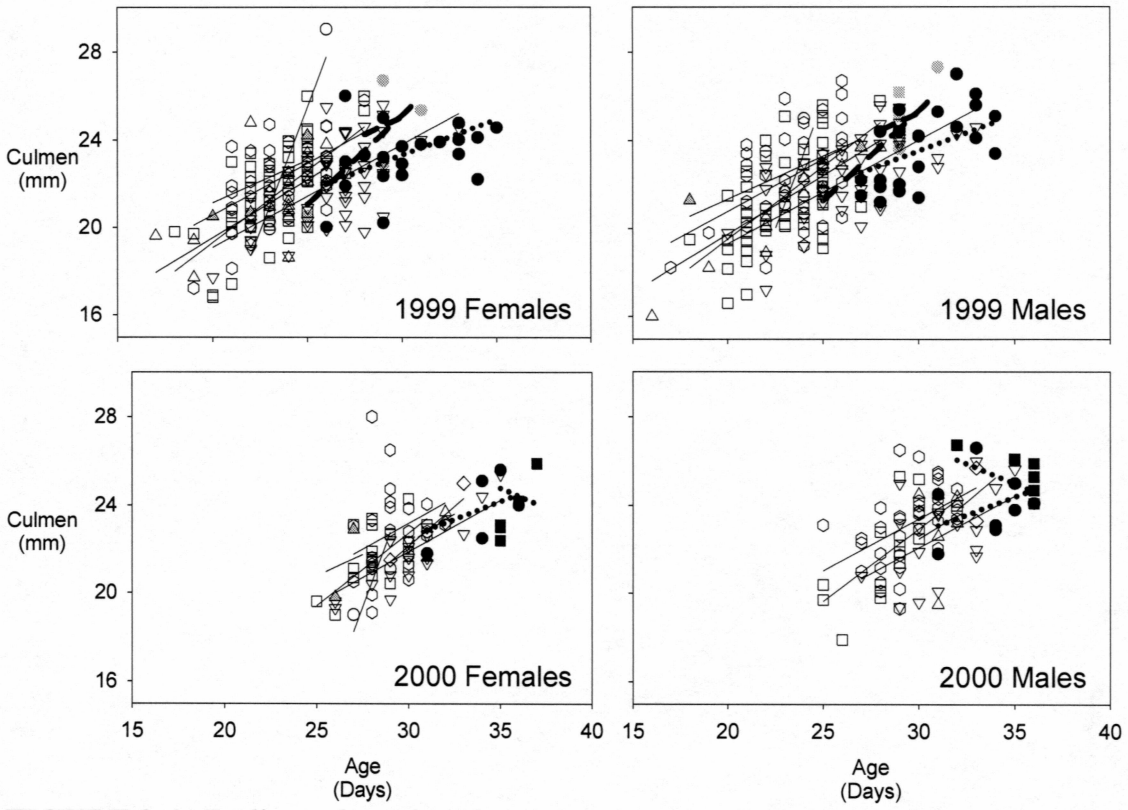

FIGURE 2-4. Gosling culmen length (mm) versus age (days). Dashed lines represent Aknerkochik River, dotted lines represent Big Slough, and solid lines represent Tutakoke River Colony. Only individual broods are presented. For presentation, gosling culmen length was averaged among brood mates within year and sex. Aknerkochik River brood rearing areas: ● Camp, ■ Peninsula. Big Slough brood rearing areas: ● Horseshoe Lake, ■ Opagaryak River. Tutakoke River Colony: ○Bend Colony, □Bend Slough, △Camp, ▽Emperor Bend, ◇Hock Slough, ⬡ Kash-Tut, and ▲Onumtuk.

TABLE 2-1. Total number of webtags and broods captured in banding drives. Two areas were sampled in each of the two satellite colonies and seven areas were sampled associated with the Tutakoke River Colony (TRC) brood rearing areas.

Study Area	Brood Rearing Area	1999		2000	
		Goslings	Broods	Goslings	Broods
Aknerkochik River	Camp	8	5	N/S	N/S
	Peninsula	3	2	N/S	N/S
Big Slough	Horseshoe Lake	53	33	14	12
	Opagaryak River	N/S	N/S	13	11
Tutakoke River	Camp	38	24	13	9
	Bend Colony	10	5	3	3
	Kash-Tut	124	72	40	27
	Bend Slough	138	91	42	30
	Hock Slough	107	64	80	60
	Onumtuk	6	5	2	2
	Emperor Bend	0	0	5	4

TABLE 2-2. AICc model selection for gosling measurements. We present the most selected model, the general model, and the highest ranking model in which one main effect has been removed.

Measurement	Model[a]	np	AICc	ΔAICc	Model Weight
Mass[b]	Y S BRA A Y*S Y*BRA S*A B	24	7911.5	0.0	0.2047
	Y S BRA A Y*BRA B	22	7912.0	0.5	0.1594
	Y S BRA A Y*S Y*BRA Y*A S*BRA S*A BRA*A B	43	7934.9	23.4	0.0000
	Y BRA A Y*BRA B	21	7940.1	28.6	0.0000
Tarsus	Y S BRA A Y*BRA BRA*A B	30	3810.1	0.0	0.3844
	Y S BRA A Y*S Y*BRA Y*A S*BRA S*A BRA*A B	43	3832.1	22.0	0.0000
	Y A BRA Y*BRA Y*A B	29	3869.0	58.9	0.0000
Culmen	Y S A BRA Y*BRA A*BRA B	30	2644.1	0.0	0.2289
	Y BRA A Y*BRA BRA*A B	29	2644.9	0.8	0.1534
	Y S BRA A Y*S Y*BRA Y*A S*BRA S*A BRA*A B	43	2664.0	19.9	0.000

[a] Y= Year, S=Sex, BRA=Brood Rearing Area, A=Age, B=Brood.

[b] We do not present 4 other models with ΔAICc<2.0 which all contained the main effects, but had different combinations of two-way interactions.

TABLE 2-3. Mixed model variance partitioning for three measurements of growth. Values are percentages of total variance within each measurement.

Effect	Measurement		
	Mass	Culmen	Tarsus
Year	13.5	11.2	11.8
Sex	1.3	0.5	11.0
Age	36.1	11.7	7.0
Brood Rearing Area	9.1	7.2	4.6
Year*Brood Rearing Area	1.4	5.5	6.4
Age*Brood Rearing Area		7.4	5.6
Brood	16.0	9.4	20.8
Residual	22.7	47.1	32.8

TABLE 2-4. Rankings of brood rearing areas by measurement and year, based on LSMeans. Lowest values indicate largest size among brood rearing areas within measurement and year. Brood rearing areas not sampled or for which no webtagged goslings were captured are denoted by N/S.

Colony	Brood Rearing Area	Mass		Tarsus		Culmen	
		1999	2000	1999	2000	1999	2000
Aknerkochik River	Camp	8	N/S	8	N/S	6	N/S
	Peninsula	6	N/S	6	N/S	4	N/S
Big Slough	Horseshoe Lake	9	9	9	9	9	7
	Opagaryak River	N/S	6	N/S	8	N/S	9
Tutakoke River	Camp	4	8	4	6	7	5
	Bend Colony	5	3	5	7	1	6
	Kash-Tut	7	7	7	4	8	8
	Bend Slough	3	5	3	5	5	3
	Hock Slough	2	4	2	3	3	1
	Onumtuk	1	2	1	2	2	2
	Emperor Bend	N/S	1	N/S	1	N/S	4

SUMMARY

We investigated two key components of reproductive success in Black Brant: synchronous hatch and location of nesting areas in relation to brood rearing areas.

The first chapter investigated possible mechanisms that may facilitate a synchronous hatch. We manipulated many nests over a two year period in ways to test a long-held hypothesis that clutches hatch synchronously due to vocalizations produced by the first laid egg to stimulate hatching of eggs from further in the laying sequence. By manipulating clutches in certain ways, we were able to tease apart environmental from genetic effects. Our data suggests that vocalization is not the primary process which synchronizes hatch in *Anatidae*, rather it appears that other factors inherent to the eggs themselves are responsible for a synchronous hatch. Additionally, we investigated growth of embryos by studying metabolic rates of eggs. Our data suggests that embryonic metabolic rate may effect development more than vocalizations between brood members in synchronizing hatch.

The second chapter investigated growth rates of Black Brant Goslings hatching in different nesting density areas. It has been hypothesized that goslings which escape density-dependence should have higher growth rates due to a lessening in competition of food resources. We studied goslings from two dispersed nesting areas and compared their growth rates to those from a main colony area for two years. After controlling for effects of age, sex, and year, we could detect differences in growth rates of goslings from the two different areas. Although our data shows variation in growth rates of goslings varies spatially, there appears to be no advantage to gosling growth rates in these

dispersed areas. Additionally, lower nest success in these dispersed areas may actually pose a cost to individuals choosing these areas, therefore these dispersed nesting birds may actually constitute a sink in the population.